PHENETICS OF *MELAMPODIUM* (COMPOSITAE, HELIANTHEAE)

Tod F. Stuessy
Department of Botany, Ohio State University,
1735 Neil Avenue, Columbus 43210

Jorge V. Crisci
Museo de Ciencias Naturales, Universidad Nacional de La Plata,
1900 La Plata, Argentina

Abstract

Phenetic analyses of 37 species of *Melampodium* are presented using cluster analysis (UPGMA) and principal components analysis (PCA). Forty-two characters are employed, 22 of which are quantitative and 20, qualitative; 26 are from reproductive parts, 15 are of vegetative parts, and 1 is chromosome base number. Six analyses are presented: three UPGMA with all characters, reproductive characters, and vegetative characters, respectively; and three PCA with the same character sets. The UPGMA with all characters and the PCA with just reproductive characters gave the best resolution of taxonomic sections and series in correlation with the previous phyletic classification of the genus. The basic framework of classification of *Melampodium* is supported, but *M. nayaritense* shows closer affinity with series *Melampodium* than with series *Sericea*. *Melampodium nutans*, shown earlier by cladistic analysis to be problematical, does not relate well phenetically to any other species.

Melampodium is a genus of 37 species that are distributed widely throughout Mexico and Central America (Stuessy 1972). It can be distinguished from its close relatives in the Melampodiinae by the inner phyllaries, which completely enclose and are fused with the achenes of the ray florets and are smooth, ridged, or tuberculate (with no spines; Stuessy 1970). Chromosomes of *Melampodium* are interesting because the genus has the longest series of haploid numbers ($n = 9$, 10, 11, 12, 18, 20, 23, 25 $\pm$ 1, 27, 30, and 33) in the subtribe and one of the longest of the Heliantheae (Stuessy 1977). Chemically, the genus is interesting because it contains different types of sesquiterpene lactones (of the class melampolides) that may be used for assessing evolutionary relationships within the genus as well as within the subtribe (Seaman et al. 1980).

Relationships among taxa of *Melampodium* already have been determined in two independent investigations. One, an intuitive classification was completed with all species placed in series and/or sections (Stuessy 1972). This has served as an initial hypothesis of relationships among all the taxa that could be tested by new data and methods. Two, a cladistic analysis of all taxa was completed and results compared with those of the previous intuitive classifi-

Madroño, Vol. 31, No. 1, 8–19, 25 January 1984

TABLE 1. CLASSIFICATION OF *Melampodium* (AFTER STUESSY 1972) SHOWING SECTIONS, SERIES, AND NUMERICAL CODES FOR SPECIES.

I. Section *Melampodium*
  A. Series *Melampodium*: 1, *M. americanum*; 2, *M. diffusum*; 3, *M. pilosum*; 4, *M. longipes*; 5, *M. linearilobum*.
  B. Series *Leucantha*: 6, *M. leucanthum*; 7, *M. cinereum*; 8, *M. argophyllum*.
  C. Series *Sericea*: 9, *M. sericeum*; 10, *M. pringlei*; 11, *M. strigosum*; 12, *M. longicorne*; 13, *M. nayaritense*.
  D. Series *Cupulata*: 14, *M. cupulatum*; 15, *M. appendiculatum*; 16, *M. sinuatum*; 17, *M. rosei*; 18, *M. tenellum*; 19, *M. glabribracteatum*.
  E. Series *Longipila*: 20, *M. longipilum*.
II. Section *Zarabellia*: 21, *M. longifolium*; 22, *M. mimulifolium*; 23, *M. gracile*; 24, *M. microcephalum*; 25, *M. paniculatum*.
III. Section *Serratura*: 26, *M. divaricatum*; 27, *M. costaricense*; 28, *M. dicoelocarpum*; 29, *M. tepicense*; 30, *M. sinaloense*.
IV. Section *Bibractiaria*: 31, *M. bibracteatum*; 32, *M. repens*.
V. Section *Rhizomaria*: 33, *M. montanum*; 34, *M. aureum*.
VI. Section *Alcina*: 35, *M. perfoliatum*; 36, *M. glabrum*; 37, *M. nutans*.

cation (Stuessy 1979). The two methods gave similar results, but some differences were detected, such as the placement of *M. nayaritense* and *M. nutans*.

During the past two decades, phenetics has been used with success to assess relationships of several plant groups (for reviews, see Sneath and Sokal 1973, Clifford and Stephenson 1975, Duncan and Baum 1981; see also Crisci 1974, Crisci et al. 1979). This method usually involves employing many non-weighted characters in different mathematical associations to produce more objective measures of affinity. These new relationships can then be compared with those obtained by other methods for a better understanding of a particular plant group (Crovello 1970).

Because phenetic classification has proven useful in other plant groups, its application to *Melampodium* seems a natural step for developing even better insights on relationships within the genus. In particular, resolutions are needed of differing putative affinities of taxa resulting from the use of intuitive and cladistic methods. The purposes of this paper, therefore, are to: (1) determine the phenetic relationships among species, series, and sections of *Melampodium* using different numerical techniques; and (2) compare these results with the previously described intuitive and cladistic relationships.

MATERIALS AND METHODS

The 37 species of *Melampodium* (Table 1) constitute the 37 Operational Taxonomic Units (OTUs) that were investigated. The characters and their states have been taken from Stuessy (1971a,b, 1972) and Keil and Stuessy (1975, 1977).

TABLE 2. CHARACTERS AND STATES USED IN THE PHENETIC ANALYSES OF *Melampodium*. All quantitative values are in mm unless otherwise noted.

VEGETATIVE CHARACTERS

PLANT: 1. Habit: annual (1), perennial (2); 2. Height (cm). STEM: 3. Orientation: prostrate or decumbent (1), ascendent (1.5), erect (2); 4. Diameter; 5. Vestiture: glabrous (1), strigose (2), pilose or tomentose (3), sericeous (4). PEDUNCLE: 6. Length (cm). LEAF: 7. Attachment: sessile or subsessile (1), petiolate (2); 8. Shape: linear, lanceolate, or oblanceolate (1), elliptic or oblong (1.5), ovate, obovate, or rhombic (2), deltate (3); 9. Length (cm); 10. Width (cm); 11. Apex: acute (1), variably acute to obtuse (2), obtuse (3); 12. Base: attenuate (1), attenuate-obtuse (1.5), obtuse (2), obtuse-auriculate (2.5), auriculate (3); 13. Vestiture (upper surface): glabrous (1), strigose (2), pilose or tomentose (3), sericeous (4); 15. Margin: serrate (1), entire to undulate (2).

REPRODUCTIVE CHARACTERS

HEAD: 16. Height; 17. Diam. OUTER INVOLUCRE: 18. Diam; 19. Bract Number; 20. Fusion: separate (1), slightly connate (1.5), connate (2); 21. Shape: linear to oblanceolate (1), ovate to rhombic (2); 22. Length; 23. Width; 24. Apex Shape: acuminate to acute (1), obtuse (2), rounded (3); 25. Vestiture (abaxial surface): glabrous (1), strigose (2), strigose-pilose (2.5), pilose, tomentose or villous (3); 26. Margin: herbaceous (1), slightly scarious (2), scarious (3). FRUIT: 27. Apical Appendage: absent (1), adaxial awn (2), abaxial hood (3); 28. Length. RAY FLORET: 29. Number; 30. Ligule Color: white (1), yellow or orange (2); 31. Ligule length; 32. Ligule width. DISC FLORET: 33. Number; 34. Corolla Diam; 35. Throat Length; 36. Tube Length. PALEA: 37. Apex Color: colorless (1), yellow or orange (2), purple (3); 38. Midrib: absent (1), weakly present (1.5), strongly present (2); 39. Vestiture of Midrib; glabrous (1), variably glabrous to pilose (1.5), pilose (2); 40. Length; 41. Width. CHROMOSOME NUMBER (basic, 42): 9, 10, 11, 12.

Data accumulation. The data consist of 42 characters scored for each of the 37 taxa (Table 2; the Basic Data Matrix is on deposit in the Ohio State University Herbarium). The set of characters includes 18 quantitative continuous, 4 quantitative discontinuous, and 20 qualitative characters. In all, 26 of the characters used are of reproductive parts and 15 are of vegetative parts. One additional character, chromosome number, was used (number 42). Chromosome numbers for several species are still unknown and these missing data are listed as NC in the Basic Data Matrix; they were ignored during computations.

Data processing. The computational work was done on an AMDAHL 470V/6II at The Ohio State University by using NT-SYS programs developed by Rohlf et al. (1971). The data were analyzed by two methods: cluster analysis and ordination. The BDM was standardized (BDMS) to remove unequal weights on characters imposed by the different scales of measurements. Details of these methods and computational procedures may be found in Sneath and Sokal (1973).

Cluster analysis. The BDMS was subjected to several agglomerative clustering procedures. Because the results were coincident, only one

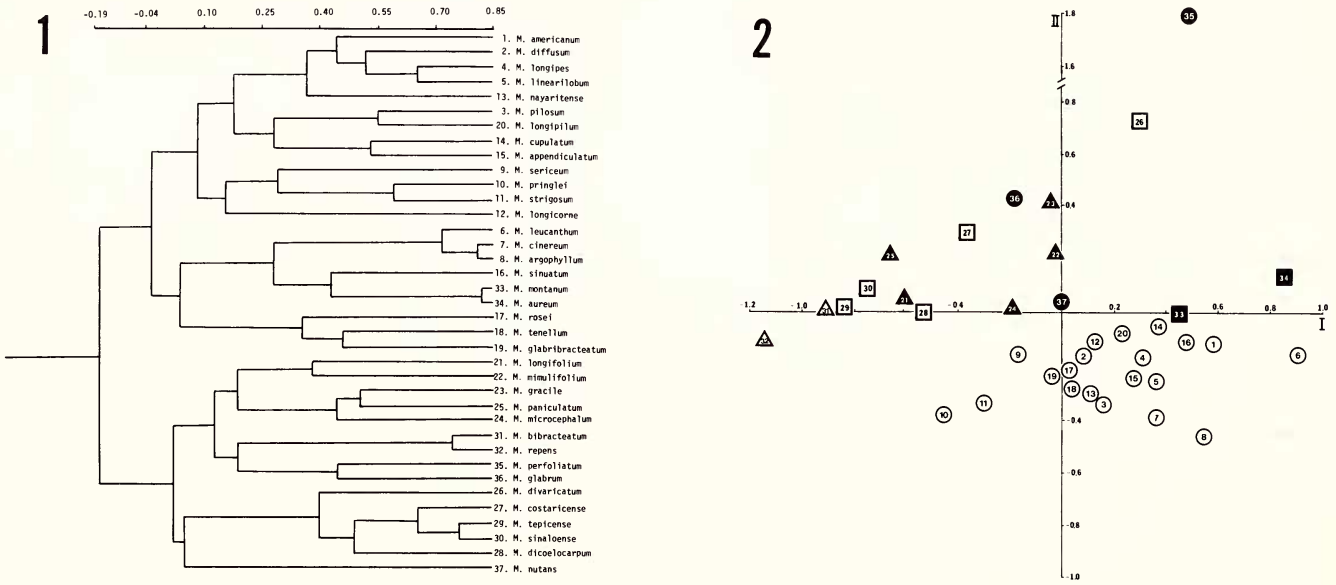
of them will be presented here. Details of these cluster analysis techniques can be found in Williams and Dale (1965), Wishart (1969), Spence and Taylor (1970), and Cormack (1971). The Pearson product-moment correlation coefficient between each pair of the 37 OTUs was calculated. The resulting OTU × OTU correlation matrix served as input in the calculation of a phenogram by the unweighted pair-group method, using arithmetic averages (UPGMA). The cophenetic correlation coefficient (r) was computed as a measurement of distortion (Sokal and Rohlf 1962). Although some criticism of this measure has been given (Farris 1969) it still seems a useful index (Sneath and Sokal 1973).

Ordination. A common technique of ordination is that of Principal Components Analysis (PCA). Accounts of the technique are given by Sneath and Sokal (1973). A character × character correlation matrix was obtained from the BDMS by calculating the Pearson product-moment correlation coefficient between each pair of the 42 characters. Principal Components Analysis was performed on the 42 × 42 character correlation matrix and the first two factors were extracted. The character factor loadings were used to calculate the factor scores or projections of OTUs in the two-factor space. To examine ordination efficiency, the Euclidean Distance between all pairs of OTUs in factor space was calculated and an OTU × OTU distance matrix was also calculated from BDMS using a Taxonomic Distance coefficient (Sneath and Sokal 1973). Both matrices were compared using the cophenetic correlation coefficient.

Results

The results of the phenetic analyses will be presented within the framework of the existing classification of *Melampodium* (Stuessy 1972), with emphasis on alignment of species in sections and series. The data will be presented for UPGMA and PCA based on the numbers and kinds of characters used for the different analyses: (1) all 42 vegetative and reproductive characters; (2) 26 reproductive characters only; and (3) 15 vegetative characters only.

Vegetative and reproductive characters. UPGMA—The previously recognized sections of *Melampodium* (Table 1) are mostly distinct with this approach (Fig. 1), with some exceptions. Section *Rhizomaria* (species 33 and 34), while connecting together well, ties closely to *M. sinuatum* (16) at the 0.42 level and is not as distinct as the other sections of the genus. Several species also seem displaced, e.g., *M. nutans* (37), which has low correlation (0.08) with nearly all other taxa. *Melampodium nayaritense* (13) was put earlier (Stuessy 1972) in series *Sericea* (9–13) but clusters closer to series *Melampodium* (1–5). *Melampodium pilosum* (3) shows greater similarity with *M. longipilum* (2), which was placed in its own monotypic



FIGS. 1 and 2. Phenetic analyses of 37 species of *Melampodium* using 42 reproductive and vegetative characters (Table 2). FIG. 1. Phenogram from UPGMA; cophenetic correlation coefficient (r) = 0.77. FIG. 2. Principal components analysis; r = 0.93.

series, rather than with its presumed position in series *Melampodium* as a close relative of *M. americanum* (1).

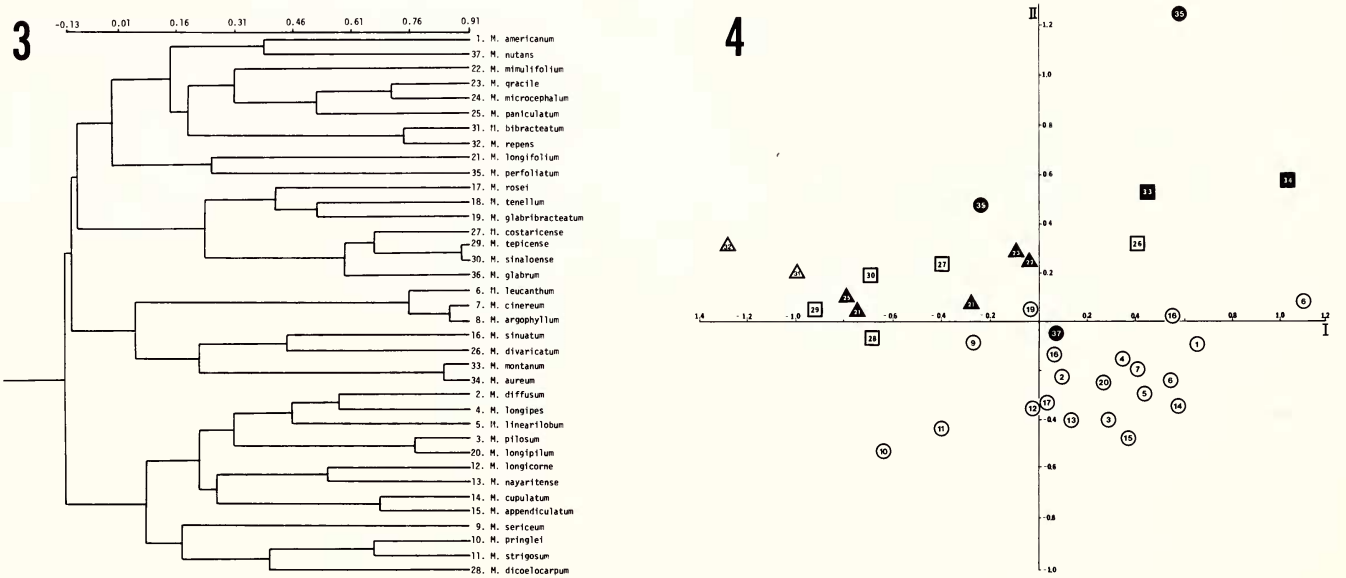
PCA—Three groups are reasonably distinct in this analysis (Fig. 2): sect. *Bibractiaria* (31, 32), sect. *Melampodium* (1–20), and sect. *Rhizomaria* (33, 34); the other three sections are intermixed. The characters that are most important for separating the taxa are in Axis I (24.05% of observed variation): numbers of ray florets, head height, head diameter, ligule length, number of disc florets, and ligule width. These features are all reproductive and quantitative. Axis II (16.04% of variation) contains primarily leaf width, plant height, leaf length, and stem diameter. All these characters are vegetative and quantitative.

Comparison of UPGMA and PCA—In both analyses, sects. *Bibractiaria* (31, 32), *Melampodium* (1–20) and *Rhizomaria* (33, 34) are clearly separated from the rest of the genus. Section *Alcina* (35–37) is not resolved in either [*M. nutans* (37) is out of place]. The other sections, *Serratura* (26–30) and *Zarabellia* (21–25) are poorly resolved in PCA but are very clear in UPGMA. The UPGMA analysis probably gives better discrimination of these two sections because it relies on many characters, whereas PCA relies on only a few factors that show a broad range of variation.

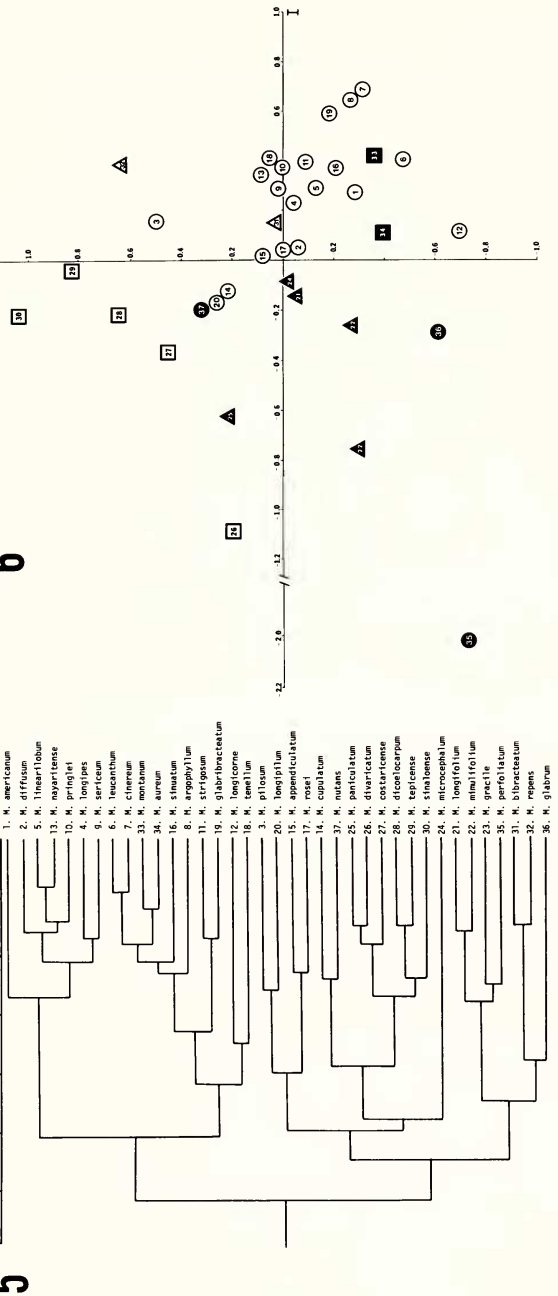
Reproductive characters only. UPGMA—In this analysis two small sections hold together well (Fig. 3): sects. *Bibractiaria* (31, 32) and *Rhizomaria* (33, 34). To a lesser extent series *Leucantha* (6, 7, 8) is also distinct. The other relationships, however, are extremely mixed and show few correlations with the previous intuitive classification.

PCA—The separation of the sections in this analysis (Fig. 4) is similar to the results with all characters (Fig. 2). Three sections, *Bibractiaria* (31, 32), *Melampodium* (1–20) and *Rhizomaria* (33, 34), are distinct. The first five important characters in Axis I (32.91% of variation) are exactly the same as those of Axis I in Fig. 2, and the degree of separation is approximately the same. Axis II contains a smaller amount of variation (13.17%) and includes fruit hood type, diameter of involucre, midrib vesture, bract width, and bract length. Again, the reproductive characters successfully delimit sects. *Bibractiaria, Melampodium,* and *Rhizomaria* and show essentially the same result, although with slightly better resolution of all sections, as with both reproductive and vegetative characters combined.

Comparison of UPGMA and PCA—The results of the two analyses on just reproductive features are very different. Sections *Bibractiaria* (31, 32) and *Rhizomaria* (33, 34) each have good internal cohesiveness, but the rest are intermixed. The phenogram also gives a very low cophenetic correlation coefficient (0.65), although the value for PCA is very high (0.93). In general, the phenogram is so distorted from the matrix of correlation coefficients that the portrayed relationships must be viewed dubiously.



FIGS. 3 and 4. Phenetic analyses of 37 species of *Melampodium* using 26 reproductive characters. FIG. 3. Phenogram from UPGMA; r = 0.65. FIG. 4. Principal components analysis; r = 0.93.



FIGS. 5 and 6. Phenetic analyses of 37 species of *Melampodium* using 15 vegetative characters. FIG. 5. Phenogram from UPGMA; r = 0.75. FIG. 6. Principal components analysis; r = 0.93.

Vegetative characters only. UPGMA—This analysis of vegetative features (Fig. 5) shows some sections more or less well resolved: *Bibractiaria* (31, 32), *Melampodium* (1–20), *Rhizomaria* (33, 34; distinct but within sect. *Melampodium*), and *Serratura* (26–30). Series *Leucantha,* however, clearly resolved in Figs. 1 and 3, is not well delimited here.

PCA—As with UPGMA, with PCA (Fig. 6) some of the sections are clear, others are not. Sections *Zarabellia* (21–25) and *Serratura* (26–30) are resolved here for the first time, indicating the importance of vegetative features in delimiting these taxa. The first four characters (all quantitative) of Axis I (27.44% variation) are the same as Axis II in Fig. 2. Characters of Axis II (16.93% variation) are all qualitative: petiolate condition of the leaves, leaf margin, stem habit, and the base of the leaves. Section *Rhizomaria* (33, 34) is for the first time not at all separated from Sect. *Melampodium* (1–20) by PCA.

Comparison of UPGMA and PCA—Both methods with vegetative data only show sects. *Serratura* (26–30), and *Zarabellia* (21–24) reasonably distinct. Sections *Melampodium* (1–20), *Bibractiaria* (31, 32), and *Rhizomaria* (33, 34), however, are better revealed in the UPGMA than in PCA (although not extremely well in either).

Discussion

In attempting to relate the new data from phenetic analyses to previous work that has been done with *Melampodium* (e.g., Stuessy 1972, 1979), the need exists to select one pattern of relationship (Figs. 1–6) for comparisons. A reasonable approach is to select the result that correlates most closely with the intuitive classification, and which has a high cophenetic correlation coefficient. Of the six different phenetic analyses, the one most similar to the previously published intuitive classification of the genus (Stuessy 1972) is UPGMA of vegetative and reproductive features (Fig. 1), which also has the highest cophenetic correlation coefficient (0.77) of the three phenograms.

Relationships among the sections. Almost all of the previously recognized sections of *Melampodium* are distinct in Fig. 1, except for *Rhizomaria* (33, 34) and *Alcina* (35–37). Section *Rhizomaria* contains two morphologically very similar species, *M. aureum* (34) and *M. montanum* (33). These cluster well together, but they also relate closely to *M. sinuatum* (16) of sect. *Melampodium.* The level of attachment of sect. *Rhizomaria* to sect. *Melampodium* is not high (0.42), but it is as high as some species within well established parts of sect. *Melampodium* [e.g., *M. americanum* (1) ties to other species of series *Melampodium* at the same level; or *M. rosei* (17) and *M. tenellum* (18), extremely close morphologically and placed in the same series *Cupulata* (14–19), are united at a lower level (0.35)].

Section *Alcina* is recognized to have three species, *M. glabrum* (36), *M. perfoliatum* (35), and *M. nutans* (37). The first two species are very similar morphologically, and they do cluster close together in Fig. 1. *Melampodium nutans,* however, clusters most closely to species of sect. *Serratura* (26–30), although at a very low level (0.08). In fact, this is the lowest association of a single species to any other species in the whole genus. There is clearly a problem, however, with the placement of *M. nutans.* Chromosomally the taxon is $n = 11$ and falls most clearly in sect. *Alcina* on that basis. (Section *Rhizomaria* also has $x = 11$; but it includes perennials, woody at the base and differing in other morphological features.) Obviously the morphological affinities of *M. nutans* are still not clear.

The phenogram also shows good resolution of sect. *Melampodium* from all other sections of the genus, except for the inclusion of sect. *Rhizomaria.* The other sections as a group cluster together suggesting that only two coordinate sections or subgenera might be recognized within the genus (Robinson 1901) rather than six. Although this viewpoint has been considered seriously, we do not believe it is the best approach because (1) the level of correlation of most sections to each other is low (Fig. 1); and (2) some of the characters have surely evolved in parallel within each of the sections. The genus has in fact undergone extensive parallel evolution as shown from cladistic studies (Stuessy 1979). This could have led to association of non-homologous features, and especially at a low level of correlation, could have caused ties that are not taxonomically meaningful.

Relationships within the sections. The relationships expressed in Fig. 1 among the species within each section are very close to those of the intuitive classification (Stuessy 1972). Section *Alcina* (35–37) is a cohesive unit, except for *M. nutans.* Section *Serratura* (26–30) is very clear with *M. tepicense* (29) and *M. sinaloense* (30) being very close. Section *Bibractiaria* (31, 32) is distinct from the other groups. Section *Zarabellia* (21–25) is a good unit but it associates at a low level (0.18). *Melampodium gracile* (23), *M. microcephalum* (24), and *M. paniculatum* (25) form a tightly-knit evolutionary unit in which artificial hybridizations have been done (Stuessy and Brunken 1979), and F_1 hybrids have been obtained in crosses between each pair of species. *Melampodium longifolium* (21) is in an isolated morphological line of sect. *Zarabellia,* a placement that seems intuitively correct. *Melampodium mimulifolium* (22), known only from the type collection, is shown as the closest relative of *M. longifolium* (Fig. 1), but the former has been regarded as simply an unusually aberrant population (or individual) of *M. gracile* (Stuessy 1972). Section *Rhizomaria* shows as a good unit on the phenogram (Fig. 1), but it occurs within sect. *Melampodium.*

Section *Melampodium* (1–20), the largest of all the sections, forms

a good unit except for the inclusion of sect. *Rhizomaria* (33, 34). Series *Melampodium* (1–5) has most species contained within except *M. pilosum,* which ties more closely to *M. longipilum* (treated as the monotypic series *Longipila*). *Melampodium nayaritense* (13) is regarded here as having stronger affinities with series *Melampodium* than with series *Sericea* as originally proposed (Stuessy 1972). Cladistic analysis (Stuessy 1979) also shows this connection and suggests even more strongly that *M. nayaritense* belongs in series *Melampodium* rather than in series *Sericea.* Series *Leucantha* (6–8), the white-rayed complex adapted to desert conditions, is a very distinct grouping. *Melampodium argophyllum* ties closest with *M. cinereum,* a position that suggests this may be the closest evolutionary tie. The flavonoid and sesquiterpene lactone chemical evidence also shows a stronger affinity in this direction (Stuessy 1971c; N. H. Fischer, pers. comm.). Stuessy (1969) treated *M. argophyllum* as a variety within *M. leucanthum*; because of its distinct morphology, it is now regarded as a recognizable species (Stuessy 1971c). Series *Cupulata* (14–19) is the most disjointed. *Melampodium cupulatum* (14) and *M. appendiculatum* (15) cluster very close to each other but are far removed from the other species (17–19) of the same series. The remaining species of the series, *M. sinuatum* (16), clusters with sect. *Rhizomaria.* Series *Sericea* (9–13) appears discrete except that *M. nayaritense* is close to series *Melampodium.*

Acknowledgments

Thanks go to the Fulbright-Hays Visiting Professor Program and The Graduate School and Department of Botany of OSU for financial support to J.V.C. for the academic year 1978–79, during which this research was initiated; to the OSU Instructional and Research Computer Center for computer time and assistance; to Marta Crisci for preparing the finished illustrations; and to the Carrera del Investigador Científico, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina, for continued support to J.V.C.

Literature Cited

Clifford, H. T. and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, NY.

Cormack, R. M. 1971. A review of classification. J. Roy. Statist. Soc. 134:321–367.

Crisci, J. V. 1974. A numerical-taxonomic study of the subtribe Nassauviinae (Compositae, Mutisieae). J. Arnold Arbor. 55:568–610.

———, J. H. Hunziker, R. A. Palacios, and C. A. Naranjo. 1979. A numerical-taxonomic study of the genus *Bulnesia* (Zygophyllaceae): cluster analysis, ordination and simulation of evolutionary trees. Amer. J. Bot. 65:133–140.

Crovello, T. J. 1970. Analysis of character variation in ecology and systematics. Ann. Rev. Ecol. Syst. 1:55–98.

Duncan, T. and B. R. Baum. 1981. Numerical phenetics—its uses in botanical systematics. Ann. Rev. Ecol. Syst. 12:387–404.

Farris, J. S. 1969. On the cophenetic correlation coefficient. Syst. Zool. 18:279–285.

KEIL, D. J. and T. F. STUESSY. 1975. Chromosome counts of Compositae from the United States, Mexico and Guatemala. Rhodora 77:171–195.

——— and ———. 1977. Chromosome counts of Compositae from Mexico and the United States. Amer. J. Bot. 64:791–798.

ROBINSON, B. L. 1901. Synopsis of the genus *Melampodium*. Proc. Amer. Acad. Arts 36:455–466.

ROHLF, F. J., J. KISPAUGH, and D. KIRK. 1971. NT-SYS: numerical taxonomy system of multivariate statistical programs. Techn. Rep. State Univ. NY, Stony Brook.

SEAMAN, F. C., N. H. FISCHER, and T. F. STUESSY. 1980. Systematic implications of sesquiterpene lactones in the subtribe Melampodiinae. Biochem. Syst. Ecol. 8:263–271.

SNEATH, P. H. A. and R. R. SOKAL. 1973. Numerical taxonomy: the principles and practice of numerical classification. W. H. Freeman, San Francisco.

SPENCE, N. A. and P. J. TAYLOR. 1970. Quantitative methods in regional taxonomy. Progr. Geogr. 2:1–64.

STUESSY, T. F. 1969. A new variety and new combination in *Melampodium* (Compositae-Heliantheae). Sida 3:348–349.

———. 1970. The genus *Acanthospermum* (Compositae-Heliantheae-Melampodiinae): taxonomic changes and generic affinities. Rhodora 72:106–109.

———. 1971a. Chromosome numbers and phylogeny in *Melampodium* (Compositae). Amer. J. Bot. 58:732–736.

———. 1971b. Chromosome studies in *Melampodium* (Compositae-Heliantheae). Madroño 20:365–372.

———. 1971c. Systematic relationships in the white-rayed species of *Melampodium* (Compositae). Brittonia 23:177–190.

———. 1972. Revision of the genus *Melampodium* (Compositae: Heliantheae). Rhodora 74:i–70, 161–219.

———. 1977. Heliantheae—systematic review. *In* V. H. Heywood, J. B. Harborne and B. L. Turner, eds., The biology and chemistry of the Compositae, p. 621–671. Academic Press, London.

———. 1979. Cladistics of *Melampodium* (Compositae). Taxon 28:179–195.

——— and J. N. BRUNKEN. 1979. Artificial interspecific hybridizations in *Melampodium* section *Zarabellia* (Compositae). Madroño 26:53–63.

WILLIAMS, W. T. and M. B. DALE. 1965. Fundamental problems in numerical taxonomy. Advan. Bot. Res. 2:35–68.

WISHART, D. 1969. FORTRAN II programs for 8 methods of cluster analysis (CLUSTAN I). Kansas Geol. Surv. Computer Contrib. 38:1–112.

(Received 11 Jan 82; accepted 17 Feb 83)